

# Intrinsic chaos and external noise in population dynamics

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## Abstract

We address the problem of the relative importance of the intrinsic chaos and the external noise in determining the complexity of population dynamics. We use a recently proposed method for studying the complexity of nonlinear random dynamical systems. The new measure of complexity is defined in terms of the average number of bits per time–unit necessary to specify the sequence generated by the system. This measure coincides with the rate of divergence of nearby trajectories under two different realizations of the noise. In particular, we show that the complexity of a nonlinear time–series model constructed from sheep populations comes completely from the environmental variations. However, in other situations, intrinsic chaos can be the crucial factor. This method can be applied to many other systems in biology and physics.

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## 1 Introduction

Recently several outstanding papers[1,2,3,4,5,6,7,8] have applied physical and mathematical methods to ecology and population dynamics. This is a very important development. In fact, interdisciplinary research can produce very significant ideas.

There exists a great controversy in ecology[9,10,11,12,13,14,15] concerning the relative importance of intrinsic factors and external environmental variations in determining populations fluctuations. In this article we address this problem using a recently proposed method[16,17] for studying the complexity of a nonlinear random dynamical system. This method characterizes the complexity by considering the rate  $K$  of divergence of nearby orbits evolving under two different noise realizations. We can show that this measure is very effective for investigating nonlinear random systems. In Ref.[14] a nonlinear time-series model is constructed from sheep populations on two islands in the St. Kilda archipelago[18,19]. We investigate the complexity of this model using the new technique. We have shown that the complexity of the system comes completely from the environmental variations. This combination of new methods is a very powerful tool for quantifying the impact of environmental variations on population dynamics and can be applied to other systems.

The paper is organized as follows: In Section 2 we recall the definition of complexity for random dynamical systems. In Section 3 we recall the definition and properties of the random sequences given in Ref.[20,21,22,23], and we compute the complexity for the random sequences and a particular random map. In Section 4 we discuss a nonlinear time-series model constructed from sheep population data and we compute the complexity for this model. In this section we also show that for a generalized model, the complexity can depend on both, the intrinsic chaos and the environmental variations. In Section 5 we briefly discuss some aspects of the problem of distinction between deterministic chaos and noise.

## 2 Complexity in random dynamical systems

Recently a new measure of complexity was introduced[16,17] in terms of the average number of bits per time-unit necessary to specify the sequence generated by the system. This definition becomes crucial in random nonlinear dynamical systems as the following

$$X_{n+1} = f(X_n, I_n), \tag{1}$$

where  $I_n$  is a random variable (e.g. noise). This measure coincides with the rate  $K$  of divergence of nearby trajectories under two different realizations of the noise. The method of calculating the Kolmogorov-Sinai entropy with the separation of two nearby trajectories with the same realization of the noise can lead to incorrect results[16,17]. The complexity of the dynamics generated by (1) can be calculated as

$$K = \lambda\theta(\lambda) + h, \quad (2)$$

where  $\lambda$  is the Lyapunov exponent of the map, which is defined as

$$\lambda = \lim_{n \rightarrow \infty} n^{-1} \ln |Z_n|, \quad (3)$$

where  $Z_{n+1} = (\partial f(X_n)/\partial X_n)Z_n$ ,  $h$  is the complexity of  $I_n$ , (which can be calculated as the Shannon entropy of the sequence  $I_n$ ), and  $\theta(\lambda)$  is the Heaviside step function. This function is defined as follows:  $\theta(\lambda) = 0$  if  $\lambda \leq 0$ ;  $\theta(\lambda) = 1$  if  $\lambda > 0$ . For a detailed explanation of the relationship between the definition of complexity as the average number of bits per time unit necessary to specify the sequence, the rate of divergence of nearby trajectories under two different realizations of the noise and the equation (2), see Ref.[36]. The definition in this form was given in the original papers[16,17]. However, in a different formalism Eq.(2) could be considered as the starting definition of  $K$ . On the other hand, there are many alternative measures of complexity. So we should check the effectiveness of this new method. In the next section, using some random sequences and a random map, we will show that the rate of divergence of nearby trajectories under two different realizations of the noise indeed can be calculated using equation (2).

### 3 Random sequences

Very recently[20,21,22,23] we have investigated explicit functions which can produce truly random numbers

$$X_n = \sin^2(\theta\pi Z^n). \quad (4)$$

When  $Z$  is an integer, function (4) is the exact solution to chaotic maps. However, when  $Z$  is a generic fractionary number, this is a random function whose values are completely independent. Using these functions (or an orthogonal set of them) we can find exact solutions to random maps as equation (1).

Let us discuss some properties of function (4). Let  $Z$  be a rational number expressed as  $Z = p/q$ , where  $p$  and  $q$  are relative prime numbers. We are

going to show that if we have  $m + 1$  numbers generated by function (4):  $X_0, X_1, X_2, X_3, \dots, X_m$  ( $m$  can be as large as we wish), then the next value  $X_{m+1}$ , is still unpredictable. This is valid for any string of  $m + 1$  numbers. Let us define the following family of sequences

$$X_n^{(k,m)} = \sin^2 [\pi (\theta_0 + kq^m) (p/q)^n], \quad (5)$$

where  $k$  and  $m$  are integer. For all sequences parametrized by  $k$ , the first  $m + 1$  values are the same. This is so because  $X_n^{(k,m)} = \sin^2 [\pi \theta_0 (p/q)^n + \pi k p^n q^{(m-n)}] = \sin^2 [\pi \theta_0 (p/q)^n]$ , for all  $n \leq m$ . Nevertheless, the next value

$$X_{m+1}^{(k,m)} = \sin^2 \left[ \pi \theta_0 (p/q)^{m+1} + \frac{\pi k p^{m+1}}{q} \right], \quad (6)$$

is unpredictable. In general,  $X_{m+1}^{(k,m)}$  can take  $q$  different values. These  $q$  values can be as different as  $0, 1/5, 1/2, \sqrt{2}/2$  or  $1$ . For  $Z$  irrational there can be an infinite number of different outcomes.

Function (4) with  $Z = 3/2$  (i.e.  $X_n = \sin^2 [\theta \pi (3/2)^n]$ ) is a solution of the following map

$$X_{n+1} = \frac{1}{2} \left[ 1 + I_n (1 - 4X_n) (1 - X_n)^{1/2} \right], \quad (7)$$

where

$$I_n = - \frac{\cos [\theta \pi (3/2)^n]}{\left\{ 1 - \sin^2 [\theta \pi (3/2)^n] \right\}^{1/2}} \quad (8)$$

if  $\sin^2 [\theta \pi (3/2)^n] \neq 1$ ; and

$$I_n = 1, \quad (9)$$

if  $\sin^2 [\theta \pi (3/2)^n] = 1$ .

A careful analysis of function  $I_n$  yields that  $I_n$  is an unpredictable function that takes the values  $\pm 1$  with equal probability. A particular realization of  $I_n$  for  $\theta = 0.77$  is the following: 1, -1, 1, -1, -1, 1, 1, -1, -1, -1, 1, -1, -1, 1, 1, -1, 1, -1, 1, ... The same analysis of Eq.(5) made above (in this case for  $Z = 3/2$ ) confirms these results. On the other hand, a statistical investigation of the outcomes of function  $I_n$  corroborates these findings. In fact, it does not matter how many past values  $I_0, I_1, I_2, \dots, I_m$  we already know, the next value

cannot be determined. It can be either 1 or -1 with the same probability. In other words,  $I_n$  behaves as a random coin toss.

Now we can check some of the results discussed by the authors of Ref.[16,17]. In the case of the random map (7)  $\lambda = \ln(3/2)$  and  $h = \ln 2$ . Thus,  $K = \ln 3$ . Here we give a brief explanation of these results. The map (7) can be re-written on the following form

$$X_{n+1} = \begin{cases} \frac{1}{2} \left[ 1 + (1 - 4X_n)(1 - X_n)^{1/2} \right], & \text{with probability } \frac{1}{2}, \\ \frac{1}{2} \left[ 1 - (1 - 4X_n)(1 - X_n)^{1/2} \right], & \text{with probability } \frac{1}{2}. \end{cases} \quad (10)$$

This is a form also compatible with the application of equation (2) (See [16,17]). After the transformation  $X_n = \sin^2(Y_n)$ , both equations

$$X_{n+1} = \frac{1}{2} \left[ 1 + (1 - 4X_n)(1 - X_n)^{1/2} \right], \quad (11)$$

and

$$X_{n+1} = \frac{1}{2} \left[ 1 - (1 - 4X_n)(1 - X_n)^{1/2} \right], \quad (12)$$

can be converted into piece-wise linear maps where the absolute value of the slope  $|dY_{n+1}/dY_n|$  is constant and equal to  $3/2$ .

Using the equation (3) for the Lyapunov exponent, we obtain the exact value  $\lambda = \ln(3/2)$ . The Lyapunov exponent is invariant with respect to the transformation  $X_n = \sin^2(Y_n)$ . If we calculate numerically the Lyapunov exponent of maps (7), (11) and (12), we also obtain the value  $\lambda = \ln(3/2)$  approximately.

Considering the properties of the sequence  $I_n$  (that takes the values 1 and  $-1$  with equal probability), it is trivial to get that  $h = \ln 2$ . Applying equation (2), we obtain  $K = \ln 3$ . All these calculations have been made using the definitions of the quantities and the algebraic structure of equation (7). Now let us consider the analytical solution of map (7):

$$X_n = \sin^2 [\theta \pi (3/2)^n]. \quad (13)$$

If we investigate equation (13), it is possible to prove that, on average, for a given  $\theta$ , nearby trajectories will separate following the law  $d \sim (3/2)^n$ , where  $d$  is the distance between the trajectories. This yields that  $\lambda = \ln(3/2)$ , which corroborates a previous result.

A more important calculation is that of  $K$ . We wish to compute the rate of divergence of nearby trajectories under two different realization of the noise. In the “language” of the exact solution (13) this is equivalent to investigate the average divergence of trajectories that are very close for  $n = 0$ , but with different values of  $\theta$  (recall that different realizations of the random variable  $I_n$  (equation (8)) are produced with different values of  $\theta$ . This analysis yields the following result  $K = \ln 3$ . And this is a corroboration of equation (2) for this system.

Now let us resort to numerical calculations. We have produced numerically 10000 values of  $X_n$  using both, the dynamical system (7) and the function (13). Then, we have computed the complexity of these sequences using the Wolf’s algorithm[24]. The result is very close to  $\ln 3$  (in fact  $K \approx 1.098$ ). Moreover, even an independent calculation of the complexity of this dynamics using different methods[24,25] produces the same result. In Ref.[25] a new method for the calculation of the complexity of a sequence is developed. This method has been shown to be very effective for the calculation of complexity of finite sequences[25,26,27,28]. We start with a sequence of values  $U_1, U_2, U_3, \dots, U_N$ ; from which we can form a sequence of vectors

$$X(i) = [U_i, U_{i+1}, \dots, U_{i+m-1}]. \quad (14)$$

Now, we will define some variables:

$$C_i^m(r) = \frac{(\text{number of } j \text{ such that } d[X(i), X(j)] \leq r)}{(N - m + 1)}, \quad (15)$$

where  $d[X(i), X(j)]$  is the distance between two vectors, which is defined as follows:

$$d[X(i), X(j)] = \max(|U_{i+k-1} - U_{j+k-1}|), \quad (k = 1, 2, \dots, m). \quad (16)$$

Another important quantity is

$$\phi^m(r) = \sum_{i=1}^{N-m+1} \frac{\ln C_i^m(r)}{N - m + 1}. \quad (17)$$

Using all these definitions, we can calculate the complexity

$$K(m, r, N) = \phi^m(r) - \phi^{m+1}(r). \quad (18)$$

This measure depends on the resolution parameter  $r$  and the *embedding* parameter  $m$ , and represents a computable framework for the “Shannon’s entropy” of a finite real sequence.

It is interesting that when we calculate numerically the complexity of the sequences produced by the map (7) and the exact solution (13) (with  $r = 0.025$ , and different  $m \geq 2$ ) we obtain  $K \approx 1.098$ .

Using functions (4) (with different values of  $Z$ ) we can also solve maps where the Lyapunov exponent is negative and, nevertheless, due to the existence of external noise, the complexity is positive. In the presence of random perturbations,  $K$  can be very different from the standard Lyapunov exponent and, hence, from the Kolmogorov–Sinai entropy computed with the same realization of the noise.

In general, if we apply the measure of complexity  $K$  to our functions (4), then we obtain the following results: for  $Z = p/q$ ,  $K = \ln p$ . If  $Z$  is irrational, the complexity is infinite. We should add some comments about these computations. When  $Z$  is integer, function (4) is equivalent to a univalued chaotic map of type  $X_{n+1} = f(X_n)$ . In this case, this measure coincides with the Kolmogorov–Sinai entropy i.e.  $K = \lambda$ . So  $\lambda = \ln Z$ . When  $Z = p/q$ , where  $p$  and  $q$  are relative primes, function (4) produces multivalued firsts-return maps [20,21,22,23]. In this case, the information lacking is not given by  $K = \lambda$ , but is larger: one loses information not only in each iteration due to  $\lambda > 0$ . One has also to specify the branch of the map  $(X_n, X_{n+1})$  in each iteration. We should apply the formula (2), where  $h$  is the entropy of the random jumps between the different branches of the map  $(X_n, X_{n+1})$ . For  $Z = p/q$ , there are  $q$  branches in the map  $(X_n, X_{n+1})$ . Investigating the properties of function (4) we arrive at the conclusion that all the branches possess the same probability in the process of jumping. This leads to the equality  $h = \ln q$ . Thus,  $K = \ln(p/q) + \ln q = \ln p$ . The complexity can be obtained by computing the separation rate of nearby trajectories evolving in two different realizations of the noise. In the case of sequences produced by function (14), this is equivalent to using two different  $\theta$  for which (at  $n = 0$ ) the trajectories are close. Such procedure exactly corresponds to what happens when experimental data are analyzed with the Wolf *et al.* algorithm [24]. When we apply the Wolf *et al.* algorithm to the sequences generated by our functions and the mentioned dynamical systems, we obtain the expected theoretical results. The complexity of the sequences produced by function (4) also can be calculated using random dynamical systems for which function (4) is the exact solution as we did in the case  $Z = 3/2$ . For different values of  $Z$ , the result is again  $K = \ln p$ .

## 4 Sheep population model

In a beautiful work Grenfell *et al.* [14] used the unusual situation of time series from two sheep populations that were very close (and so, they shared approximately the same environmental variation as for example rain, temperature,

etc) but which were isolated from each other, i.e. these populations did not interact, in order to study the interaction between noise and nonlinear population dynamics. They found high correlations in the two sheep populations on two islands in the St. Kilda archipelago. They were able to express  $X_{n+1}$  as a function of the previous population size:  $X_{n+1} = f(X_n) + \epsilon_{n+1}$ , where  $\epsilon_n$  represents the noise, which is related to the environmental variables ( $n$  is the discrete time). Here  $X_n = \log N_n$ , where  $N_n$  is the population number. They fit a nonlinear self-exciting threshold autoregressive (SETAR) model[29,30,31] to the Hirta island (one of the islands of the St. Kilda archipelago) time series. The best-fit model is

$$\begin{aligned} X_{n+1} &= a_0 + b_0 X_n + \epsilon_{n+1}^{(0)}, & X_n \leq c, \\ X_{n+1} &= a_1 + \epsilon_{n+1}^{(1)}, & X_n > c, \end{aligned} \tag{19}$$

where  $c = 7.066$ ;  $a_0 = 0.848$ ;  $b_0 = 0.912$ ;  $\sigma_0 = 0.183$ ;  $a_1 = 7.01$ ;  $\sigma_1 = 0.293$ . Here  $\sigma_{0,1}$  is the variance of  $\epsilon_n$ . The noise  $\epsilon_n$  is defined as a sequence of independent and identically distributed normal random numbers with mean 0 and variance  $\sigma$ . The model captures the essential features of the time-series, including the map  $X_{n+1}$  versus  $X_n$ . Now we apply the measure of complexity  $K$  (Eq.(2)) to the model given by equation (19). It is straightforward to show that  $\lambda < 0$ . This can be done even analytically using equation (3). Thus, the complexity of the dynamical system (19) is  $K = h$ , where  $h$  is the complexity of the noise  $\epsilon_n$ . That is, all the complexity of this dynamical system comes completely from the environmental variations. We could say that, in this case, the extrinsic environmental variations are much more important than the intrinsic factors in determining population size fluctuations.

This result confirms the results of Ref.[14]. However, we should note that their research is based on the very particular situation where we have synchronization of two population fluctuations at separate, but not too distant locations.

Here we should explain briefly how Grenfell *et al.*[14] obtained their results. They found that the fluctuations in the sizes of the two populations are remarkably synchronized over a 40-year period. They explain this synchronization using the fact that the two populations are exposed simultaneously to the same environmental variations. Assuming that the same model applies to both islands, they use it to estimate the level of correlation in environmental noise required to generate the observed synchrony in population fluctuations. They found that very high levels of noise correlation are needed to generate the observed correlation between the sheep populations on the two islands. They also studied observed large-scale meteorological covariates like monthly wind, rain and temperature. From this analysis they conclude that the extrinsic influences are very important in this particular case of population dynamics.



On the other hand, our method can be applied to any other population dynamics. Even if we have only one isolated population in the same region. The research program is the following: the data should be fitted by a SETAR model and, after that, the complexity can be calculated using equation (2). In fact, many nonlinear population models can be approximated by a SETAR model. This is a very clear theoretical result. It does not depend on further statistical assumptions or approximate investigations. Once we have reconstructed the model from the data (and this is a step that we cannot avoid in any other method), we can prove rigorously that the Lyapunov exponent is negative and that all the complexity comes from the external random perturbations. Our results explain why the environmental variations are more important in this particular case. This is due to the density-dependent relationship  $X_{n+1} = f(X_n)$ . In fact, for other animal populations the best-fit model can be very different. The form of the density dependence is crucial. For instance, suppose that the best-fit model is similar to that presented in Ref.[15]:

$$X_{n+1} = \begin{cases} r + X_n + \epsilon_{n+1}^{(1)}, & X_n \leq c, \\ (r + bc) + (1 - b)X_n + \epsilon_{n+1}^{(2)}, & X_n > c. \end{cases} \quad (20)$$

Here we should add a short explanation of the origin of Eq.(11). In Ref.[32] Mayrand Smith and Slatkin discuss the so-called MSS model

$$N_{n+1} = \frac{RN_n}{(1 + N_n/N_c)^b}, \quad (21)$$

where  $N_n$  is the population size at time  $n$ ,  $R$  is the maximal net population growth rate,  $b$  is a measure of the strength of the density dependent reduction of the net population growth rate, and  $N_c$  is the carrying capacity (that is, the maximum population size that can be sustained by the area under study). If we introduce the transformation  $X_n = \ln N_n$  (and the effect of noise), we can obtain equation (20) as an approximation, where  $r = \ln R$ ,  $c = \ln N_c$  (See Ref.[15]). However, in the same way as Eq.(19), Eq.(20) can be obtained as a SETAR model reconstruction using a given time-series of the evolution of certain animal population. In general, as pointed out by Stenseth and Chan[15], many nonlinear population models may, on the log-scale, be approximated by a dynamical system similar to equation (20).

For large values of parameter  $b$ , the Lyapunov exponent can be positive. In this case, both the intrinsic and the external factors contribute to the variability of the dynamics. Moreover, it can be that the intrinsic chaotic factors are the most important in determining population fluctuations. Nevertheless, we have shown that randomness is crucial in ecological models.

## 5 Chaos and noise

In the research presented in this paper the question of chaos or noise is very relevant both in the problems related to the random functions and in the problems of characterizing experimental time-series.

We should say here that recently several important papers have been dedicated to the question of distinguishing between generic deterministic chaos and noise[33,34,35,36,37]. Several limitations have been found for the usual methods that are based on the calculation of the Lyapunov exponent and the Kolmogorov–Sinai entropy[37]. Many of the practical problems are related to the fact that these quantities are defined as infinite time averages taken in the limit of arbitrary fine resolution.

New very strong methods have been developed based on different concepts. Some of these methods[33,34,35] are based on the differences in the predictability when time-series is analyzed using prediction algorithms.

In Ref.[37] this problem is solved by introducing the  $(\epsilon, \tau)$  entropy  $(h(\epsilon, \tau))$ , which is a generalization of the Kolmogorov–Sinai entropy with finite resolution  $\epsilon$ , and where the time is discretized by using a time interval  $\tau$ .

If the Kolmogorov–Sinai entropy can be calculated exactly and is finite, then we can assure that the time-series was generated by a deterministic law. Usually the  $(\epsilon, \tau)$ –entropy displays different behaviors as the resolution is varied. According to these different behaviors one can distinguish deterministic and stochastic dynamics. We can even define a certain range of scales for these phenomena.

For a time-series long enough, the entropy can show a saturation range. For  $\epsilon \rightarrow 0$ , one observes the following behaviors:  $h(\epsilon) \approx \text{const}$  for a deterministic system, whereas  $h(\epsilon) \sim -\ln \epsilon$  for a stochastic system. In general, predictability can be considered as a fundamental way to characterize complex dynamical systems[36]. We have used a method developed in the papers[33,34,35], in order to investigate numerically the randomness of functions (4). This technique is very powerful in distinguishing chaos from random time series. The idea of the method is the following. One can make short-term predictions that are based on a library of past patterns in a time series. By comparing the predicted and actual values, one can make distinctions between random sequences and deterministic chaos. For chaotic (but correlated) time series, the accuracy of the nonlinear forecast falls off with increasing prediction-time interval. On the other hand, for truly random sequences, the forecasting accuracy is independent of the prediction interval. If the sequence values are correlated, their future values may approximately be predicted from the behavior of past values that are similar to those of the present. For uncorrelated random sequences

the error remains constant. The prediction accuracy is measured by the coefficient of correlation between predicted and observed values. For deterministic chaotic sequences this coefficient falls as predictions extend into the future. Suppose we have a sequence  $u_1, u_2, \dots, u_N$ . Now we construct a map with the dependence of  $u_n(\text{predicted})$  as a “function” of  $u_n(\text{observed})$ . If we have a deterministic chaotic sequence, this dependence is almost a straight line, i.e.  $u_n(\text{predicted}) \approx u_n(\text{observed})$  (when the forecasting method is applied for one time step into the future). When we increase the number of time steps into the future, this relation becomes worse. The decrease with time of the correlation coefficient between predicted and actual values has been used to calculate the largest Lyapunov exponent of a time series[34]. We have applied this method of investigation to our functions(4)[20]. When  $Z$  is an integer ( $Z > 0$ ), the method shows that the function (4) behaves as a deterministic chaotic system. If  $Z$  is irrational, the correlation coefficient is independent of the prediction time. Even when the method is applied with prediction time interval  $m = 1$ , the correlation coefficient is zero (the map  $(u_n(\text{predicted}), u_n(\text{observed}))$  covers completely the square  $0 \leq x \leq 1, 0 \leq y \leq 1$ , showing no patterns). This shows that the corresponding time series behaves as a random sequence. When  $Z = p/q$ , function (4) behaves as a system with both, deterministic chaos and noise. In this case, it is better to complement the study with several alternative methods.

As pointed out by Cencini *et al.*,[37], all these methods have in common that one has to choose certain length scale  $\epsilon$  and a particular embedding dimension  $m$ . Thus the scenarios discussed in [36,37] can be very useful in all the investigations aimed at the distinction between chaos and noise.

## 6 Conclusion

Cohen[38] has reported that the solutions of chaotic ecological models have power spectra with increasing amplitudes at higher frequencies. This is in contrast with the spectra presented in natural populations which are dominated by low-frequency fluctuations. Some authors[11] suggest that this is a manifestation of the interaction between biotic factors and climatic factors. This problem shows the difficulties in deciding whether natural populations fluctuations are determined by internal biological mechanisms or they are mostly the result of external environmental forcing. We think that our results can help to shed light on this issue. Recently there have been reports[39,40] on population dynamics where the variability of the population originates from both deterministic chaos and stochastic processes. The complexity given by equation (2) can help to determine the relative weight of both factors. In fact, the understanding of the interaction of both deterministic and stochastic processes is crucial to model correctly the dynamics of an ecological system.

We propose a combined approach to this issue: the SETAR model and the new method for calculating complexity. In the particular case of the sheep populations in the St. Kilda archipelago, it seems that the population fluctuations are influenced mostly by frequent environmental variations which include monthly wind, rain, temperature, food shortage and parasitism.

We believe that the ideas and methods used in the present article can be applied to other nonlinear random systems in biology and physics.

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